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Review

A global synthesis of the impacts of urbanization on bird dawn choruses

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Urbanization drives changes in acoustic communication systems in some animal species. Noise and light pollution are among the main urban factors known to disrupt the timing and structure of avian singing behaviour. Despite our understanding of the ways in which urbanization can drive variations in avian acoustic communication, our ability to generalize the underlying causes of such variation and its consequences is still limited. Here, we reviewed the literature focused on the study of avian dawn choruses in urban settings at a global scale. Our findings reveal that avian dawn chorus research has focused on the impact of anthropogenic noise on dawn chorus traits (i.e. timing, peak, song output, song frequencies); relationships between light pollution and chorus timing; the effects of temperature, cloudiness, moonlight and natural light on chorus timing; relationships between nocturnal noise and light, and dawn chorus timing; the effects of chemical pollution and supplementary feeding on dawn chorus activity; and ecological patterns of dawn choruses in soundscapes across urban–non-urban gradients. We identified important knowledge gaps in the study of avian dawn choruses in urban settings and thus suggest future research directions, including frameworks (e.g. the urbanization intensity gradient) and consideration of a wider array of urban conditions and variables. Given the complexity of urban settings, we encourage further studies to address the role that all sources of pollution can have on avian acoustic communication at dawn. Additionally, a central question to resolve is whether the function of avian dawn choruses in urban areas differs, and if so how, from non-urban counterparts. Given that most research has been performed across Holarctic cities and towns, studies from tropical and subtropical regions are needed if we aim to understand the phenomenon globally. Finally, studies at the community- and soundscape-level across cities could advance understanding of the way in which urban birds use the acoustic space during the most critical singing time period, dawn.

Keywords: acoustic signalling, chorusing, soundscape ecology, urban ecology, urban pollution.

INTRODUCTION

Sounds are a fundamental property of nature, providing relevant information about the status of biodiversity (Pijanowski *et al.* 2011). Sounds emitted by animals have become one of the most studied proxies in the assessment and understanding of the ecological impacts of human activities (Slabbekoorn 2018, Burivalova *et al.* 2019). However, there are still important gaps in our understanding of how the sum of sounds emitted by biological,

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geophysical and anthropogenic sources (i.e. soundscapes) are affected by landscape transformation and how human-driven forces shape their organization and dynamics (Pijanowski *et al.* 2011, Krause & Farina 2016).

One important component of soundscapes is animal chorus (i.e. vocalizations emitted by multiple individuals of the same or different species at the same time in response to common diel cues; Burt & Vehrencamp 2005, Catchpole & Slater 2008). Such choruses are common in many wildlife groups, including birds, fish, mammals, insects and shrimps (Farina & Ceraulo 2017). By signalling in choruses, animals communicate by broadcasting important information about their spatial location, territory quality and mate attraction (Kacelnik & Krebs 1982, Burt & Vehrencamp 2005, Greenfield 2005, Schel & Zuberbühler 2012, Farina & Ceraulo 2017).

Recent studies suggest that the disruption of animal chorus timing and organization is a consequence of increasing levels of anthropogenic noise in both terrestrial and aquatic ecosystems (Pijanowski *et al.* 2011, Krause & Farina 2016, Farina & Ceraulo 2017). However, it is not yet fully understood how anthropogenic activities influence animal chorusing at the population- and community- level across ecosystems worldwide. Urban ecosystems, especially, are characterized by multiple stressors, including chemical pollution, increasing temperature levels, high levels of anthropogenic noise (in both amplitude and frequency domains), artificial light at night (ALAN) and human presence, all of which can affect wildlife, with physiological, ecological and behavioural responses emerging to deal with such stressful conditions (see Isaksson 2018 and references therein). In fact, innovative problem-solving, personality and phenotypic plasticity have been identified as important adjustments to urban life (Gil & Brumm 2014, Isaksson 2018). Evidence of the behavioural plasticity of acoustic phenotypes (i.e. overall temporal, spectral and amplitude characteristics of an acoustic signal; Slabbekoorn 2013) of urban birds has increased in the last decade, due its association with the two dominant drivers in urban environments: anthropogenic noise and artificial light pollution (Slabbekoorn 2013, Shannon *et al.* 2016, Gaston *et al.* 2017).

As predicted by the acoustic adaptation hypothesis (AAH), differences in habitat structure could shape the acoustic properties of animal communication (Morton 1975). Due to the environmental heterogeneity of urban settings (e.g. differing land-uses, urbanization intensity gradients, spatio-temporal artificial light and noise variations), together with their acoustic complexity (Warren *et al.* 2006), the AAH has provided a fundamental framework to understand how animals deal with predominant anthropogenic noise by adjusting their acoustic phenotype to increase the effectiveness of their acoustic signals (Slabbekoorn & Peet 2003, Luther & Baptista 2010, Phillips *et al.* 2020). Some bird species have been shown to deal with anthropogenic noise in cities by adjusting the amplitude, minimum frequency, syntax and timing of songs (Slabbekoorn & Peet 2003, Brumm 2004, Luther & Baptista 2010, Slabbekoorn 2013, Gil *et al.* 2015, Bermúdez-Cuamatzin *et al.* 2018). Moreover, recent evidence highlights the biological consequences of artificial light for birds, particularly their physiology and behaviour (Gaston *et al.* 2017). For example, artificial light can affect circadian rhythms through the disruption of melatonin cycles (Dominoni, 2015), leading to earlier dawn choruses in light-polluted areas (Fuller *et al.* 2007, Da Silva *et al.* 2016, Hopkins *et al.* 2018).

Chorusing (i.e. acoustic display involving three or more members of a social unit, including both males and females) is a widespread, complex behaviour among birds, occurring in at least 1830 species (~ 18% of all known bird species), including both passerines and non-passerines (Tobias *et al.* 2016). Among these acoustic displays, dawn choruses are a conspicuous but little understood trait of avian natural history (Catchpole & Slater 2008, Gil & Llusia 2020). Typically, this behaviour is defined as a peak of singing activity performed by different bird species starting around first light, with a gradual decline towards sunrise (Staicer *et al.* 1996, Catchpole & Slater 2008, Gil & Llusia 2020). This complex phenomenon can also be described at different levels: individuals within species, species within communities (Gil & Llusia 2020) and communities within soundscapes (Farina & Ceraulo 2017). A functional framework based on 12 hypotheses has been proposed to explain the existence of dawn choruses, focused on intrinsic, environmental and social factors (Staicer *et al.* 1996, Gil & Llusia 2020). Intrinsic factors include the circadian cycles of testosterone, and environmental factors include low predation risk, better acoustic transmission, inefficient foraging at

lower ambient light levels, unpredictable overnight conditions and body condition (Kacelnik & Krebs 1982, Staicer *et al.* 1996, Hutchinson, 2002, Thomas *et al.* 2002, Brown & Handford 2003, Catchpole & Slater 2008, Gil & Llusia 2020). The role of dawn choruses has been suggested to be mostly social, although there are additional hypotheses (Kacelnik & Krebs 1982, Staicer *et al.* 1996, Burt & Vehrencamp 2005). In this sense, dawn choruses could be pragmatically assessed as interactive communication networks (i.e. senders both broadcast and eavesdrop information, Burt & Vehrencamp 2005), in which males convey information for mate attraction and mate guarding, territorial ownership, and resolution of social relationships among neighbours (Staicer *et al.* 1996, Burt & Vehrencamp 2005, Tobias *et al.* 2016).

In this review, we identify the main research topics and general patterns so far addressed in studies of avian dawn choruses in urban settings, and provide new insights for future research directions better to understand the effect of urbanization on dawn choruses. To do this, we combined bibliometrics and systematic mapping tools (Nakagawa *et al.* 2019) to synthesize the main publication trends across years and the current state of the knowledge on urban bird dawn choruses across the globe.

LITERATURE SEARCH AND ANALYSIS

We performed a systematic search in Web of Science (WoS; all Databases; www.webofscience.com) including publications from 1966 to 2018 and using the following advanced search Boolean operator string: TS = ((urban* OR city) AND (*bird OR avian OR songbird) AND (dawn OR morning OR awakening OR onset OR sunrise) AND (chorus* OR singing OR song OR call OR calls OR calling OR birdsong OR bird-song OR 'acoustic signalling' OR 'diel patterns' OR 'singing activity' OR 'dawn chorus' OR 'dawn singing' OR 'singing behav*' OR 'first song' OR 'chorus onset' OR 'earlier singing' OR 'chorus composition' OR 'chorus structur*' OR 'chorus duration' OR 'chorus time' OR 'song duration')). After screening the 55 documents retrieved in this search, we kept 17 that met the scope of this review and saved these as a BibTex file for further bibliometric analysis.

To broaden and complement our search, we searched for related literature in Google Scholar (https://scholar.google.com), which focuses on not only peer-reviewed journal publications, but also theses, dissertations, monographs, book chapters and conference publications (Haddaway *et al.* 2015). The search string we used in Google Scholar (GS) was: 'dawn chorus' AND 'bird' OR 'songbird' OR 'urbanisation' OR 'urbanization', which retrieved 3680 documents. After examining the title of the first 300 retrieved from GS results to exclude those beyond our scope (following suggestions of Haddaway *et al.* 2015), 127 remained of interest for this review. We screened all studies from WoS and GS for further analysis, considering those which were focused on dawn choruses or singing behaviour at dawn and were performed in urban areas (verifying the geographical coordinates to corroborate the location of the studied locations in doubtful cases). We excluded some studies that simulated urban conditions, such as those focused on artificial light at night and anthropogenic noise in study areas that are not urban (e.g. forest plots) (e.g. Halfwerk & Slabbekoorn 2009, Da Silva *et al.* 2016, 2017). This added 27 publications to those identified in the Web of Science, giving a total of 44 publications focused on urban bird dawn choruses.

We assessed publication trends with the following criteria: publication year, title, subject categories (i.e. noise, ALAN, singing behaviour, noise–ALAN, meteorological factors, soundscape, supplementary feeding, chemical pollution), biogeographical region, country, city, study type (i.e. observational, correlational, experimental), study level (i.e. population, community, soundscape), and framework (i.e. intra-urban, intra-urban greenspaces, peri-urban greenspaces, urban non-urban gradient, urban-forest contrast). We considered three types of studies:

- *observational*: reporting naturalistic descriptions of singing behaviour at dawn,
- *correlational*: focused on relationships between dawn chorus traits and environmental variables,
- *experimental*: assessing the effect of a controlled variable (i.e. anthropogenic noise, light pollution, food supply), on the dawn chorus with the aim of disentangling the mechanisms behind associations.

We also collated information on the studied bird species in order to assess their phylogenetic representation and biogeographical distribution. For this, we extracted phylogenetic trees for the

studied species pool from the Birdtree database (Jetz *et al.* 2012). We then generated a distribution of 1000 randomly selected permutations of the phylogeny (Hackett backbone), and used 'treeannotator' software (Drummond *et al.* 2012) to obtain the best supported phylogenetic tree based on a maximum clade credibility phylogeny approach. To assess general global topic trends, we performed a word cloud representation (i.e. an infographic tool to summarize the general trends through the frequency of keywords of a given topic) considering publication titles. Finally, we explored relationships among main topics by exploring the links between author's keywords of each study using word co-occurrence networks ('bibliometrix' R package; Aria & Cuccurullo 2017). This approach allows visualization of the conceptual structure of a given topic based on the links between concepts through keyword co-occurrences (Aria & Cuccurullo 2017). In these networks, the nodes represent the keywords scaled by the number of studies that mentioned them, and the edges represent the co-occurrence of different keywords among studies.

URBAN BIRD DAWN CHORUS

General patterns

Although the study of avian dawn choruses in urban areas began in the 1960s, the number of publications has risen in the last decade (Fig. 1). In general, studies have focused on:

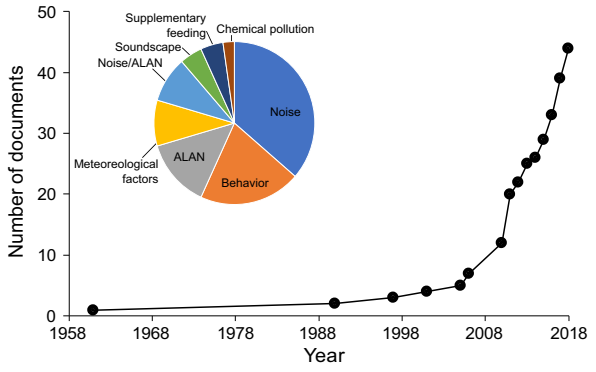

Figure 1. Number of accumulated documents focused on bird dawn choruses published by year. Pie chart shows the proportion of studies by main topic.

- the impact of anthropogenic noise on song structure and timing (e.g. Bergen & Abs 1997, Dorado-Correa *et al.* 2016, Marini *et al.* 2017, Sierro *et al.* 2017),
- relationships between ALAN and dawn chorus onsets (e.g. Bergen & Abs 1997, Miller 2006, Kempenaers *et al.* 2010, Da Silva & Kempenaers 2017),
- variation in singing behaviour at dawn related to time of day (e.g. Leopold & Eynon 1961, Shihan 2010, Singh *et al.* 2019),
- the influence of temperature, cloud, moonlight and sunlight on the onset of dawn choruses (Hasan 2010, 2011, Ki *et al.* 2015, Hasan & Badri 2016, Lee *et al.* 2017),
- relationships between noise, ALAN and dawn chorus timing (Bergen & Abs 1997, Nordt & Klenke 2013),
- effects of chemical pollution and supplementary feeding on dawn chorus activity (Cuthill & Macdonald 1990, Gorissen *et al.* 2005, Saggese *et al.* 2011).

Interestingly, there has been a recent emergence of novel approaches, such as soundscape ecology recognizing avian dawn choruses as a central component of urban soundscapes (Gage *et al.* 2017, Ross *et al.* 2018).

Most of the reviewed studies have focused on relationships between urbanization intensity and dawn chorus at the population-level (80%), whereas the community- and soundscape-levels have remained largely unexplored (Fig. 2). Moreover, 59% of the studies focused on ecological aspects (e.g. comparing variations on dawn chorus behaviour between urban and adjacent non-urban areas) and 41% performed bioacoustics assessments (e.g. evaluating how birds dealt with masking issues). Most studies were correlational (64%), assessing relationships between traffic noise, light pollution and urban intensity with dawn chorus onset (Miller 2006, Shihan 2010, Da Silva & Kempenaers 2017, Sierro *et al.* 2017), song output (Bergen & Abs 1997, Singh *et al.* 2011, Marini *et al.* 2017) and song frequency adjustments (Ripmeester *et al.* 2010, Potvin & Parris 2012, Rios-Chelen *et al.* 2013), but did not control for potentially confounding factors, such as differences in noise and light pollution, or variation between urban and non-urban birds (Da Silva *et al.* 2017). A minority of studies were experimental (20%), focusing on the effects of traffic noise on chorus

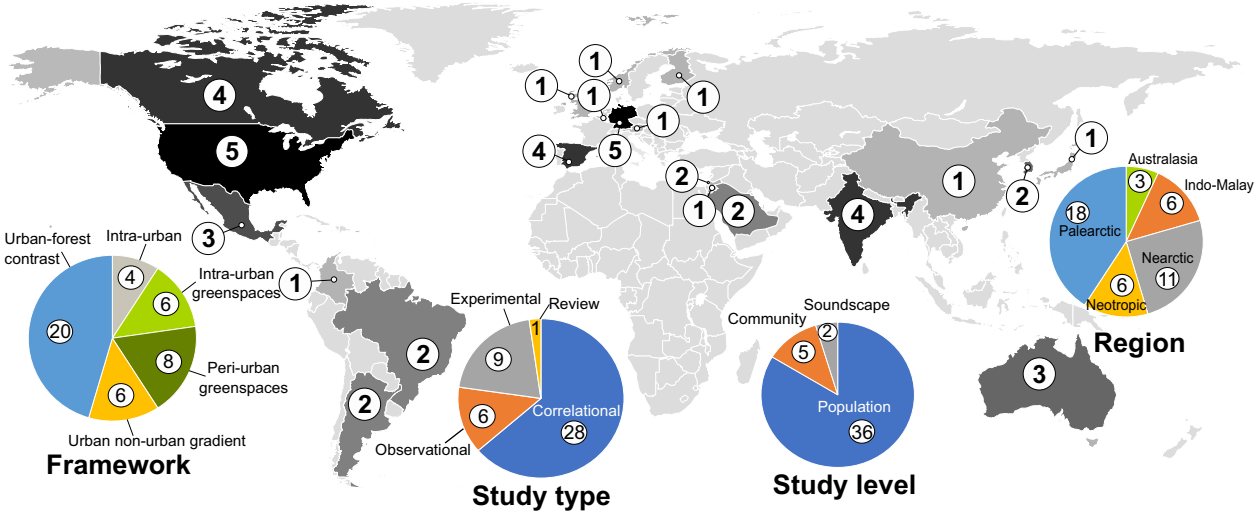

Figure 2. Map depicting the number of avian dawn chorus studies by country. The intensity of grey scale indicates the frequency of studies. Pie charts represent the proportion of studies according to the classified framework, study type, study scale and climatic region.

timing (Rivera-Caceres *et al.* 2011, Arroyo-Solís *et al.* 2013, LaZerte *et al.* 2017), the consequences of ALAN for song performance and reproductive success (Kempenaers *et al.* 2010) and the effects of supplementary feeding on chorus timing (Cuthill & Macdonald 1990, Saggese *et al.* 2011). Notably, some studies have documented the singing behaviour routines of birds at dawn (e.g. Pizo & Silva 2001, Hasan 2011, Singh *et al.* 2019).

Most research has been conducted across the Palearctic and Nearctic regions, especially the USA, Germany, Canada and Spain (Table 1). However, there was also a high representation of studies from India (Fig. 2) and recent studies from Argentina, Brazil, Palestine, Saudi Arabia and South Korea (Fig. 2). Studies were performed in 51 urban centres (Table 1), five of which lead in the number of publications ($n = 3$): Kelowna and Kamloops (Canada), Brisbane (Australia), Haridwar (India) and Mexico City (Mexico). The size of the urban settings where studies have been performed ranges from small villages (e.g. Kfar Ruppin, Israel) to megacities, such as Delhi (India). However, most studies have been performed in small- to medium-sized cities (74.5%), followed by large cities (17.7%) and megacities (7.8%) (i.e. Delhi, Mexico City, Bogotá).

The most frequent framework followed in urban bird dawn chorus studies has been to compare dawn chorus traits (i.e. timing, peak, song output, song frequencies) between urban bird populations or communities and their non-urban (usually forest) counterparts (Fig. 2; Table 1; Leopold & Eynon 1961, Bergen & Abs 1997, Miller 2006, Potvin *et al.* 2011, Sierro *et al.* 2017, Alquezar 2018). Peri-urban and intra-urban greenspaces have also received some attention, in particular through experimental studies of the effects of supplementary feeding and ALAN on dawn chorus timing (Cuthill & Macdonald 1990, Kempenaers *et al.* 2010, Saggese *et al.* 2011), and effects of traffic noise on dawn chorus singing routines in urban areas (Rivera-Caceres *et al.* 2011, Rios-Chelen *et al.* 2013, Lee *et al.* 2017, Manzanares Mena & Macías Garcia 2018).

However, in contrast to general urban bird literature (see Marzluff 2017 and references therein), there are few studies based on urban–rural (or 'non-urban') gradients. Although urbanization gradients have been a widely used in urban ecology (McDonnell & Pickett 1990), their use in studies of avian dawn choruses is relatively recent and is focused at the non-urban end of such gradients. Some studies have assessed avian acoustic activity across urbanization gradients, suggesting an inverse correlation between the acoustic diversity of avian dawn choruses and urbanization intensity (e.g. Ross *et al.* 2018). Moreover, urban–non-urban gradient studies have also provided experimental evidence of the effects of ALAN and anthropogenic

Table 1. Summary of the global studies of avian dawn choruses in urban settings

Source	City, Country	Region	Level	Species	Study type	Framework	Major findings
Leopold & Enyon 1961	Madison, USA	Nearctic	Population	*Agelaius phoeniceus, Cardinalis cardinalis, Chordeiles minor, Contopus virens, Dumetella carolinensis, Geothlypis trichas, Icterus galbula, Passerina cyanea, Phasianus colchicus, Melospiza melodia, Myiarchus crinitus, Scolopax minor, Sialia sialis, Spizella passerina, Spizella pusilla, Sturnella magna, Toxostoma rufum, Troglodytes aedon, Turdus migratorius, Vireo gilvus, Zenaida macroura,*	Correlational	Urban-forest-contrast	Urban birds showed delayed dawn chorus in contrast to their rural counterparts
Cuthill & Macdonald 1990	Oxford, UK	Palearctic	Population	*Turdus merula*	Experimental	Peri-urban greenspaces	Food supplied birds showed earlier dawn song and greater song output
Bergen & Abs 1997	Dortmund, Germany	Palearctic	Population	*Cyanistes caeruleus, Fringilla coelebs, Parus major*	Correlational	Urban-forest-contrast	ALAN and noise pollution drive earlier dawn chorus onset in urban birds
Pizo & Silva 2001	Campinas, Brazil	Neotropic	Population	*Eupetomena macroura*	Observational	Intra-urban greenspaces	Reported a short daily period of vocal display in a hummingbird species restricted to just before sunrise
Gorissen *et al.* 2005	Flanders, Belgium	Palearctic	Population	*P. major*	Correlational	Urban-forest-contrast	Birds exposed to heavy metal pollution had smaller repertoire size and lower song rate during dawn chorus
Miller 2006	Schuylkill Haven, Arlington, Madison, USA	Nearctic	Population	*T. migratorius*	Correlational	Urban-forest-contrast	Birds had earlier dawn chorus onsets in urban areas with high levels of ALAN
Warren *et al.* 2006	Baltimore, USA	Nearctic	Community		Review	Intra-urban	Suggested a potential overlapping of avian dawn chorus with high noise levels during morning rush hours
Kempenaers *et al.* 2010	Vienna, Austria	Palearctic	Population	*C. caeruleus, Erithacus rubecula, F. coelebs, P. major, T. merula*	Experimental	Peri-urban greenspaces	ALAN levels affected the reproductive success in urban songbirds

(continued)

Table 1. (continued)

Source	City, Country	Region	Level	Species	Study type	Framework	Major findings
Ripmeester *et al.* 2010	Leiden, Netherlands	Palearctic	Population	*C. caeruleus, E. rubecula, F. coelebs, P. major, T. merula*	Correlational	Urban-forest-contrast	Variations on dawn song structure of urban birds to anthropogenic noise was determined by the individual responses
Saggese *et al.* 2011	Oslo, Norway	Palearctic	Population	*P. major*	Experimental	Peri-urban greenspaces	Birds under continuous food supply conditions showed a delayed dawn chorus onset
Shihan 2010	New Taipei City, Taiwan	Indo-Malay	Population	*Myiophonus insularis*	Correlational	Urban-forest-contrast	ALAN disrupted the singing behaviour
Trimboli 2010	Bowling Green, USA	Nearctic	Population	*Thryothorus ludovicianus*	Correlational	Urban-forest-contrast	Urban birds sang more than their rural counterparts
Hasan 2010	Tulkarem, Kfar Ruppin, Palestine, Israel	Palearctic	Population	*Passer domesticus, Pycnonotus xanthopygos, T. merula*	Observational	Urban-forest-contrast	Dawn chorus start times differed among species
Hasan 2011	Riyadh, Tulkarem, Saudi Arabia, Palestine	Palearctic	Population	*P. domesticus, P. xanthopygos, T. merula*	Correlational	Intra-urban	Earlier dawn chorus onset was related to variations on environmental temperature instead light and noise pollution levels
Laiolo 2011a	Bahía Blanca, Argentina	Neotropic	Population	*Zonotrichia capensis*	Correlational	Urban-forest-contrast	Urban birds changed the structure of their dawn chorus song
Laiolo 2011b	Bahía Blanca, Argentina	Neotropic	Population	*Z. capensis*	Correlational	Urban-forest-contrast	Urbanization leads to acoustic plasticity of dawn songs
Potvin *et al.* 2011	Melbourne, Adelaide, Sydney, Grafton, Brisbane, Hobart, Canberra, Australia	Australasia	Population	*Zosterops lateralis*	Correlational	Urban-forest-contrast	Birds in noisier urban settings showed high song frequencies and slower songs
Rivera-Caceres *et al.* 2011	Mexico City, Mexico	Nearctic	Population	*Pyrocephalus rubinus*	Experimental	Intra-urban greenspaces	Long songs during dawn chorus was an honest signal of bird males
Sethi *et al.* 2011	Haridwar, India	Indo-Malay	Population	*Saxicola caprata*	Experimental	Peri-urban greenspaces	The presence or absence of a mate did not influence male dawn singing behaviour

(continued)

Table 1. (continued)

Source	City, Country	Region	Level	Species	Study type	Framework	Major findings
Singh *et al.* 2011	Delhi, India	Indo-Malay	Community	*Acridotheres tristis, Cinnyris asiaticus, Columba livia, Copsychus saularis, Corvus splendens, Streptopelia decaocto, Pycnonotus cafer*	Observational	Intra-urban greenspaces	Avian dawn chorus in urban settings ranged between 1000Hz to 3500Hz and showed high levels of energy (60dB to 70dB)
Sethi *et al.* 2012	Haridwar, India	Indo-Malay	Population	*S. caprata*	Observational	Peri-urban greenspaces	Dawn chorus played an important role in maintenance of social relationships among neighbours
Potvin & Parris 2012	Melbourne, Adelaide, Sydney, Grafton, Brisbane, Hobart, Canberra, Australia	Australasia	Population	*Z. lateralis*	Correlational	Urban-forest-contrast	Birds modified their dawn song structure to increase transmission in urban noisier environments
Arroyo-Solís *et al.* 2013	Sevilla, Spain	Palearctic	Population	*Chloris chloris, Carduelis carduelis, Sturnus unicolor, P. domesticus, Serinus serinus, S. decaocto*	Experimental	Intra-urban	Experimental traffic noise changed dawn chorus timing, with some urban bird species singing earlier
Nordt & Klenke 2013	Leipzig, Germany	Palearctic	Population	*T. merula*	Correlational	Urban non-urban gradient	Noise and light pollution disrupted the natural patterns of dawn singing in birds leading to earlier activity
Rios-Chelen *et al.* 2013	Mexico City, Mexico	Nearctic	Population	*P. rubinus*	Correlational	Intra-urban greenspaces	Birds in noisier territories sang at a higher pitch than those in less noisy locations
Ki & Cho 2014	Wonju, South Korea	Palearctic	Population	*P. major*	Correlational	Urban-forest-contrast	Light pollution drives earlier dawn chorus in urban settings
Gil *et al.* 2015	Madrid, Barcelona, Valencia, Málaga, Berlin, Spain, Germany	Palearctic	Population, Community	*Acrocephalus scirpaceus*, *C. carduelis*, *C. chloris*, *Cettia cetti*, *Cuculus canorus*, *C. caeruleus, E. rubecula, Luscinia megarhynchos, P. major, S. serinus, Sylvia atricapilla, T. merula, T. philomelos*	Correlational	Urban-forest-contrast	Birds near airports showed earlier dawn chorus onsets

(continued)

Table 1. (continued)

Source	City, Country	Region	Level	Species	Study type	Framework	Major findings
Ki *et al*. 2015	Miryang, Korea	Palearctic	Population, Community	*Corvus corone, Dendrocopos kizuki, Hypsipetes amaurotis, P. major, Phasianus colchicus, Phoenicurus auroreus, Pica pica, Picus canus, Schoeniclus elegans,*	Correlational	Peri-urban greenspaces	Dawn chorus start times were a species-specific trait
LaZerte *et al*. 2015	Prince George, Quesnel, Kelowna, Vancouver, Williams Lake, Kamloops, Kelowna, Canada	Nearctic	Population	*Poecile atricapillus, Poecile gambeli*	Experimental	Urban non-urban gradient	Birds depended of previous experience to noise to adjusts their dawn chorus songs
Dominoni *et al*. 2016	Berlin, Germany	Palearctic	Population, Community	*C. caeruleus, Columba palumbus, Dendrocopos major, E. rubecula, F. coelebs, Sitta europaea, Troglodytes troglodytes, P. major, T. merula, T. philomelos,*	Correlational	Urban-forest-contrast	Some bird species adjusted the timing of dawn chorus, being earlier in response to aircraft noise
Dorado-Correa *et al*. 2016	Bogotá, Colombia	Neotropic	Population	*Z. capensis*	Correlational	Urban-forest-contrast	Birds had earlier dawn chorus onsets in noisier urban areas independently of light pollution levels
Hasan & Badri 2016	Riyadh, Saudi Arabia	Palearctic	Population	*P. domesticus*	Correlational	Intra-urban	Longer days (short nights) and high temperature drives earlier dawn chorus onsets
LaZerte *et al*. 2016	Prince George, Quesnel, Kelowna, Vancouver, Canada	Nearctic	Population	*P. atricapillus*	Experimental	Urban non-urban gradient	Only birds that live in noisy territories shifted songs upwards in immediate response to experimental noise
Da Silva & Kempenaers 2017	Oulu, Starnberg, Granada, Finland, Germany, Spain	Palearctic	Population	*C. caeruleus, E. rubecula, P. major, F. coelebs, T. merula*	Correlational	Urban-forest-contrast	Songbirds adjusted earlier dawn chorus onset to variation on natural and artificial light levels
Gage *et al*. 2017	Brisbane, Australia	Australasia	Soundscape		Observational	Peri-urban greenspaces	The dawn and dusk choruses were detected by acoustic indices

(continued)

Table 1. (continued)

Source	City, Country	Region	Level	Species	Study type	Framework	Major findings
LaZerte *et al.* 2017	Williams Lake, Kamloops, Kelowna, Canada	Nearctic	Population	*P. gambeli*	Experimental	Urban non-urban gradient	Experimental manipulation of noise showed that birds in noisier territories shifted to use more songs, whereas birds in quieter sites used more calls
Lee *et al.* 2017	Los Angeles, USA	Nearctic	Community	*Corvus brachyrhynchos, Corvus corax, Junco hyemalis, Melozone crissalis, S. passerina, Pheucticus melanocephalus, Pipilo maculatus, Sayornis nigricans, Sialia mexicana, Spinus psaltria, Thryomanes bewickii, Tyrannus verticalis, T. migratorius, Tyrannus vociferans, Z. macroura*	Correlational	Intra-urban greenspaces	Natural light levels and noise pollution were related to the earlier dawn choruses
Marini *et al.* 2017	Kamloops, Canada	Nearctic	Population	*P. gambeli*	Correlational	Urban non-urban gradient	Males in more urbanized habitats had earlier chorus onsets, greater vocal output, and longer song duration, compared to rural counterparts
Sierro *et al.* 2017	Madrid, Spain	Palearctic	Population	*T. merula*	Correlational	Urban-forest-contrast	Birds near to airports sang earlier and increased the time singing at dawn
Alquezar 2018	Brasilia, Campinas, Salvador, Brazil	Neotropic	Population, Community	*Camptostoma obsoletum, Cyclarhis gujanensis, Elaenia chiriquensis, Elaenia cristata, Elaenia flavogaster, Furnarius rufus, Lepidocolaptes angustirostris, Myiarchus swainsoni, Neothraupis fasciata, Pitangus sulphuratus, Tangara sayaca, Tyrannus melancholicus, Troglodytes musculus, Turdus leucomelas, Z. capensis*	Correlational	Urban-forest-contrast	Species-specific advances and delays in dawn chorus onset were related to airport noise

(continued)

Table 1. (continued)

Source	City, Country	Region	Level	Species	Study type	Framework	Major findings
Edenborg 2018	Linköping, Sweden	Palearctic	Population	*C. caeruleus, E. rubecula, F. coelebs, P. major, T. troglodytes, T. merula*	Correlational	Urban-forest-contrast	Earlier singing birds were more affected by ALAN than late singing birds
Manzanares Mena & Macías Garcia 2018	Mexico City, Mexico	Neotropic	Community	*Amazilia beryllina, Aphelocoma californica, Atlapetes pileatus, Cardellina rubra, Catherpes mexicanus, Cynanthus latirostris, Dryobates scalaris, Geothlypis nelsoni, Haemorhous mexicanus, Hirundo rustica, M. melodia, P. domesticus, Passerina caerulea, P. melanocephalus, Psaltriparus minimus, Quiscalus mexicanus, Setophaga townsendi, Spinus pinus, Spizella atrogularis, S. passerina, T. bewickii, T. migratorius, Turdus rufopalliatus, T. vociferans, Vireo huttoni*	Correlational	Intra-urban greenspaces	Species richness was negatively affected by increasing anthropogenic noise
Ross *et al.* 2018	Okinawa, Japan	Indo-Malay	Soundscape, population	*Corvus macrorhynchos, Halcyon coromanda, H. amaurotis, Otus elegans, Gallirallus okinawae*	Correlational	Urban non-urban gradient	Acoustic diversity and the bioacoustic index reflected avian chorus dynamics across urban gradients
Singh *et al.* 2019	Haridwar, India	Indo-Malay	Population	*Copsychus saularis*	Observational	Peri-urban greenspaces	Dawn chorus occurred before sunrise

noise on dawn chorus onset and song structure, showing short-term responses of avian acoustic phenotype (i.e. increasing minimum song frequencies, advancing dawn chorus onset, increasing song rate) in noisy urban areas (Nordt & Klenke 2013, LaZerte *et al.* 2016, 2017, Marini *et al.* 2017). Finally, a few studies have been conducted exclusively in intra-urban areas, exploring the relationships between dawn chorus timing and traffic noise (Arroyo-Solís *et al.* 2013), as well as environmental factors such as temperature (Hasan 2010, Hasan & Badri 2016).

Focal species

There were 111 species included in the reviewed studies (Table 1, Fig. 3). However, a few species dominated as models to understand the relationships between urbanization and dawn choruses. In the Palearctic region, songbirds, particularly the Great Tit *Parus major* (n = 10 studies), Common Blackbird *Turdus merula* (n = 10), Eurasian Blue Tit *Cyanistes caeruleus* (n = 6), European Robin *Erithacus rubecula* (n = 5), House Sparrow *Passer domesticus* (n = 5) and Common Chaffinch *Fringilla coelebs* (n = 5) were the most frequent model species. In the Nearctic region, the American Robin *Turdus migratorius* (n = 4), Mountain Chickadee *Poecile gambeli* (n = 3) and Chipping Sparrow *Spizella passerina* (n = 3) were the most frequent. The only Neotropical songbird in the dataset was the Rufous-collared Sparrow *Zonotrichia capensis* (n = 4). Most reviewed studies focused on single species pertaining to just a few family clades: Paridae, Muscicapidae, Turdidae, Passeridae, Fringillidae and Passerellidae (Fig. 3).

Topic trends

Word clouds based on publication titles indicated the most representative key subjects such as dawn chorus singing behaviour, anthropogenic noise, artificial light pollution and the effects of urbanization on song frequency adjustments (Fig. 4). However, the co-word network analysis added further information on the relationships between topics in the study of urban dawn choruses. Author keywords showed a tightly connected network with five main research clusters and four peripheral ones that were not connected with the core (Fig. 5). The core cluster (depicted in purple, Fig. 5) comprises the influence of anthropogenic drivers, such as noise and light pollution, on temporal shifts of dawn choruses (Bergen & Abs 1997, Miller 2006, Gil *et al.* 2015), as well as variations in dawn song rates (Dominoni *et al.* 2016) and dawn song repertoire sizes (Trimboli 2010). The second cluster (depicted in red, Fig. 5) focuses on the behavioural plasticity of territorial songs (Laiolo 2011a, 2011b), variations in song length and the role of learning to deal with fluctuating noise levels (LaZerte *et al.* 2015, 2016, 2017). The third cluster (depicted in orange, Fig. 5) comprises studies focused on experimental evidence of song plasticity driven by anthropogenic noise (e.g. Ripmeester *et al.* 2010, Arroyo-Solís *et al.* 2013) and how tolerance to noise drives structure of urban bird communities (Manzanares Mena & Macías Garcia 2018). The fourth cluster (depicted in blue, Fig. 5) includes the role of cultural evolution in acoustic adaptation to urban settings (Potvin *et al.* 2011, Potvin & Parris 2012). The fifth cluster (depicted in green, Fig. 5) consists of studies focused on song frequency adjustments to noise (Rivera-Caceres *et al.* 2011, Rios-Chelen *et al.* 2013). Finally, the peripheral clusters include studies describing the ecological patterns of soundscapes across urban–non-urban gradients (Gage *et al.* 2017, Ross *et al.* 2018), the impact of ALAN on fitness through mate selection (Kempenaers *et al.* 2010), behavioural descriptions of singing activity at dawn (Pizo & Silva 2001) and the impacts of chemical pollution on dawn song repertoire size (Gorissen *et al.* 2005).

In the following sections, we summarize the major findings regarding the effects on urban bird dawn choruses of anthropogenic noise, light pollution, chemical pollution, meteorological factors and supplementary feeding, and the implications of these for soundscape ecology.

ECOLOGICAL DRIVERS OF AVIAN URBAN DAWN CHORUS

Anthropogenic noise

The effects of noise pollution on avian urban ecology have been well studied (e.g. Slabbekoorn 2013, Halfwerk *et al.* 2018). Urban soundscapes are characterized by high levels of low-frequency anthropogenic noise (2 kHz). Some bird species respond by adjusting song frequency, in particular increasing minimum frequency to avoid acoustic masking (Slabbekoorn & Peet 2003, Ripmeester *et al.* 2010, Potvin *et al.* 2011, Rivera-Caceres

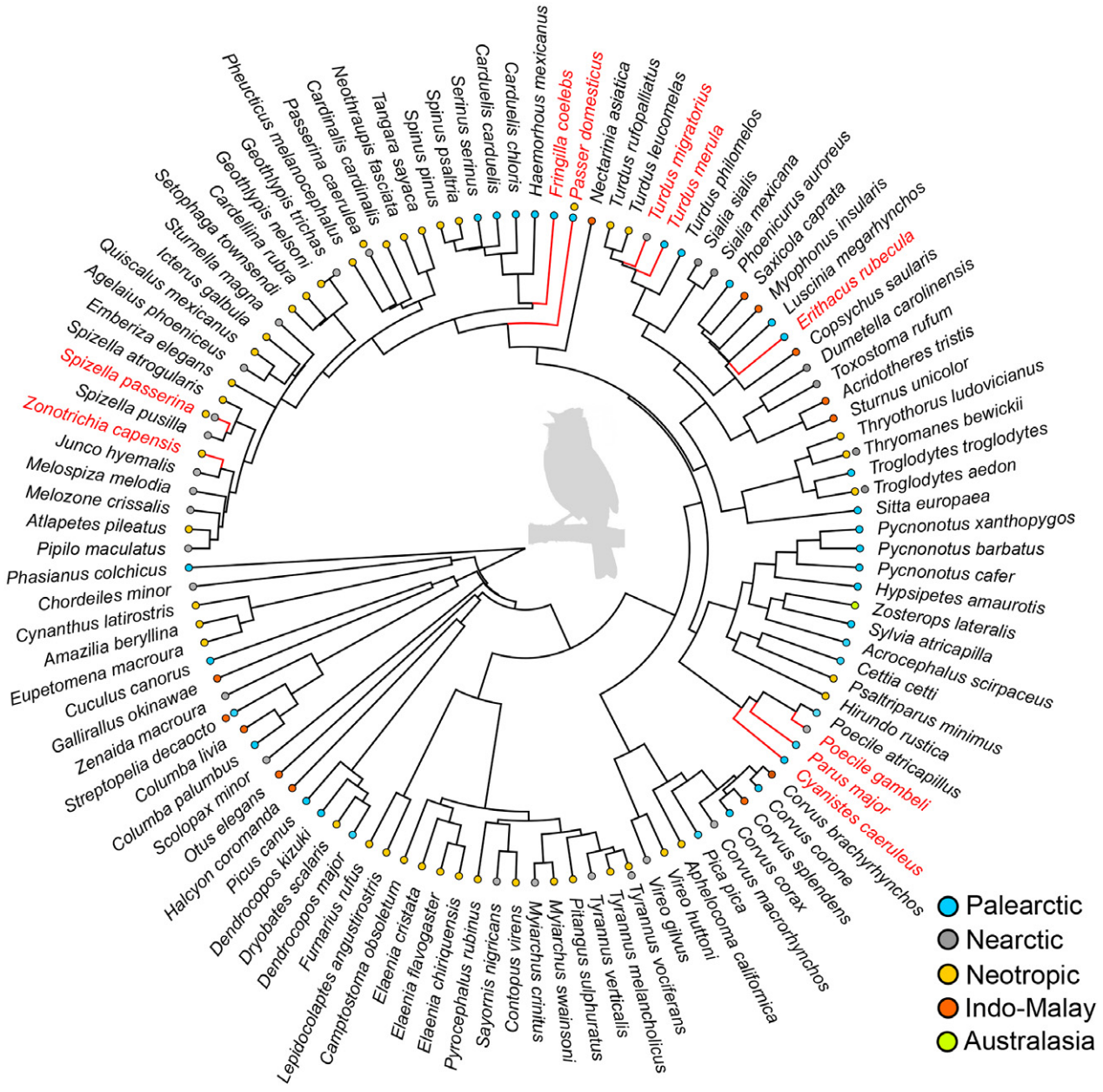

Figure 3. Phylogenetic tree of 111 bird species based on which dawn choruses have been studied in urban settings. Colour points represent the biogeographical region where the species was studied. Red labels and branches indicate the most studied species (> three studies).

et al. 2011, Rios-Chelen *et al.* 2013). This behavioural response has been supported by further experimental work suggesting rapid acoustic adjustments in song structure to intermittent traffic noise (Arroyo-Solís *et al.* 2013, LaZerte *et al.* 2017, Bermúdez-Cuamatzin *et al.* 2018, Halfwerk *et al.* 2018). Changes in the timing of dawn singing routines have also been recorded (Bergen & Abs 1997, Fuller *et al.* 2007, Nordt & Klenke 2013, Dominoni *et al.* 2016). In general, urban birds tend to advance their dawn chorus onset and chorus peak times due to increasing levels of traffic noise and pedestrian activity during rush hours (Bergen & Abs 1997, Warren *et al.* 2006, Arroyo-Solís *et al.* 2013, Dorado-Correa *et al.* 2016, Marín-Gómez & MacGregor-Fors 2019).

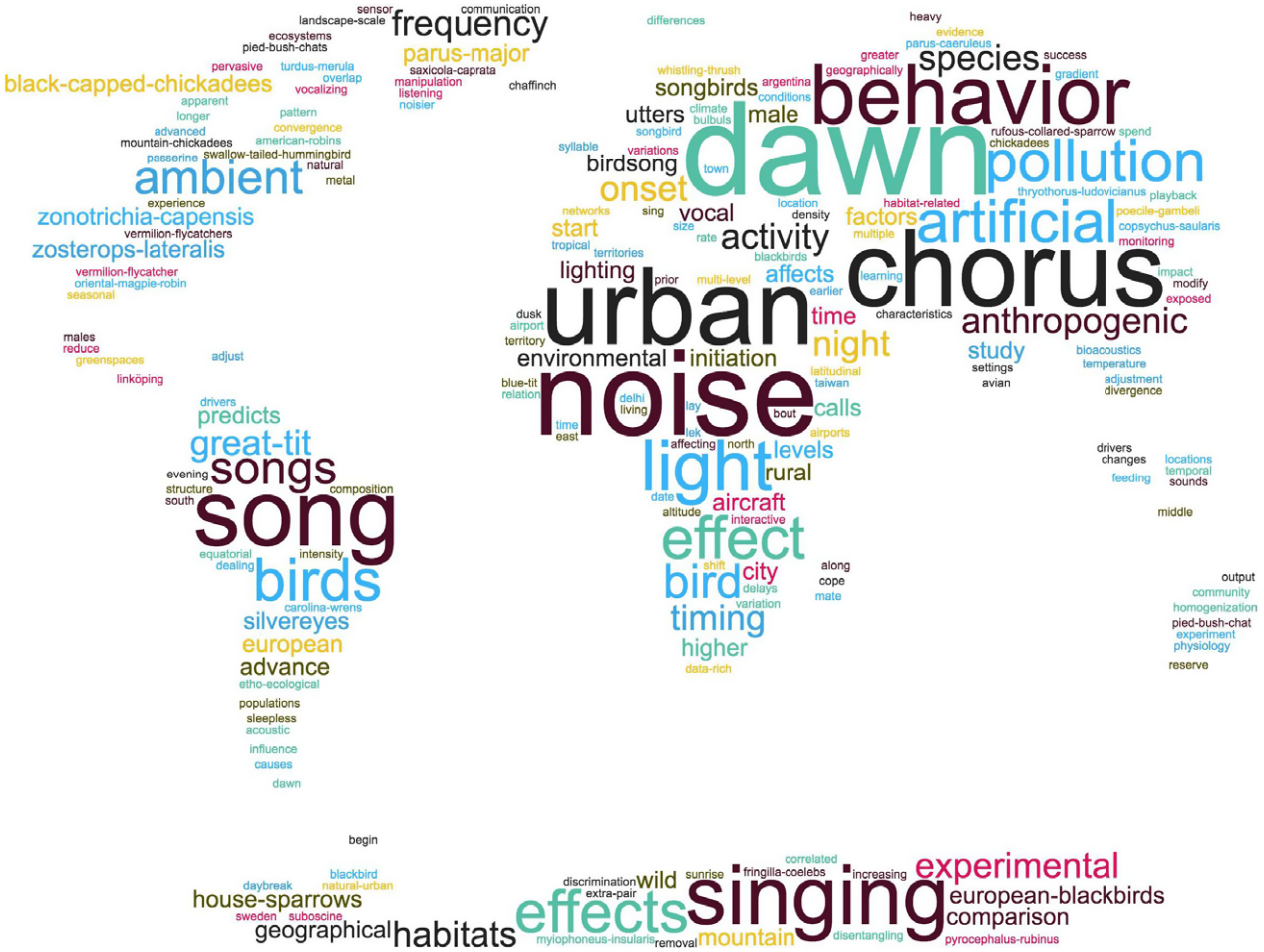

Figure 4. Word cloud synthesizing the most frequently studied topics of urban bird dawn choruses based on the title of the reviewed publications.

Urban birds can also change the song repertoire used during the dawn chorus. For instance, birds in noisier urban settings produce both slower (Potvin *et al.* 2011) and longer songs (Rivera-Caceres *et al.* 2011, LaZerte *et al.* 2017, Marini *et al.* 2017), and sing more than their non-urban counterparts (Trimboli 2010). Moreover, urbanization can also result in changes to the syntax of dawn songs (LaZerte *et al.* 2017). For example, urban Mountain Chickadees have shown higher vocal output (i.e. number of songs in a given period of time) compared with non-urban males, but also can shift to using more songs, whereas males in quiet areas produce more calls (LaZerte *et al.* 2017, Marini *et al.* 2017).

In accordance with the predictions of the AAH (Morton 1975), studies have also focused on understanding how birds increase signal transmission in urban environments through acoustic plasticity of territorial dawn songs. There is good evidence that urban birds in noisier territories sing at a higher pitch than their counterparts living in quieter locations (Potvin *et al.* 2011, Laiolo 2011a, 2011b, Rios-Chelen *et al.* 2013, LaZerte *et al.* 2016). However, such short-term adjustments can also be related to previous noise experience of individual birds (Ripmeester *et al.* 2010, LaZerte *et al.* 2015). For example, Black-capped Chickadees *Poecile atricapillus* living in noisy areas increase the pitch of their territorial songs in response to experimental noise, suggesting that prior experience and learning processes can influence immediate adjustments to fluctuating noise levels (LaZerte *et al.* 2016).

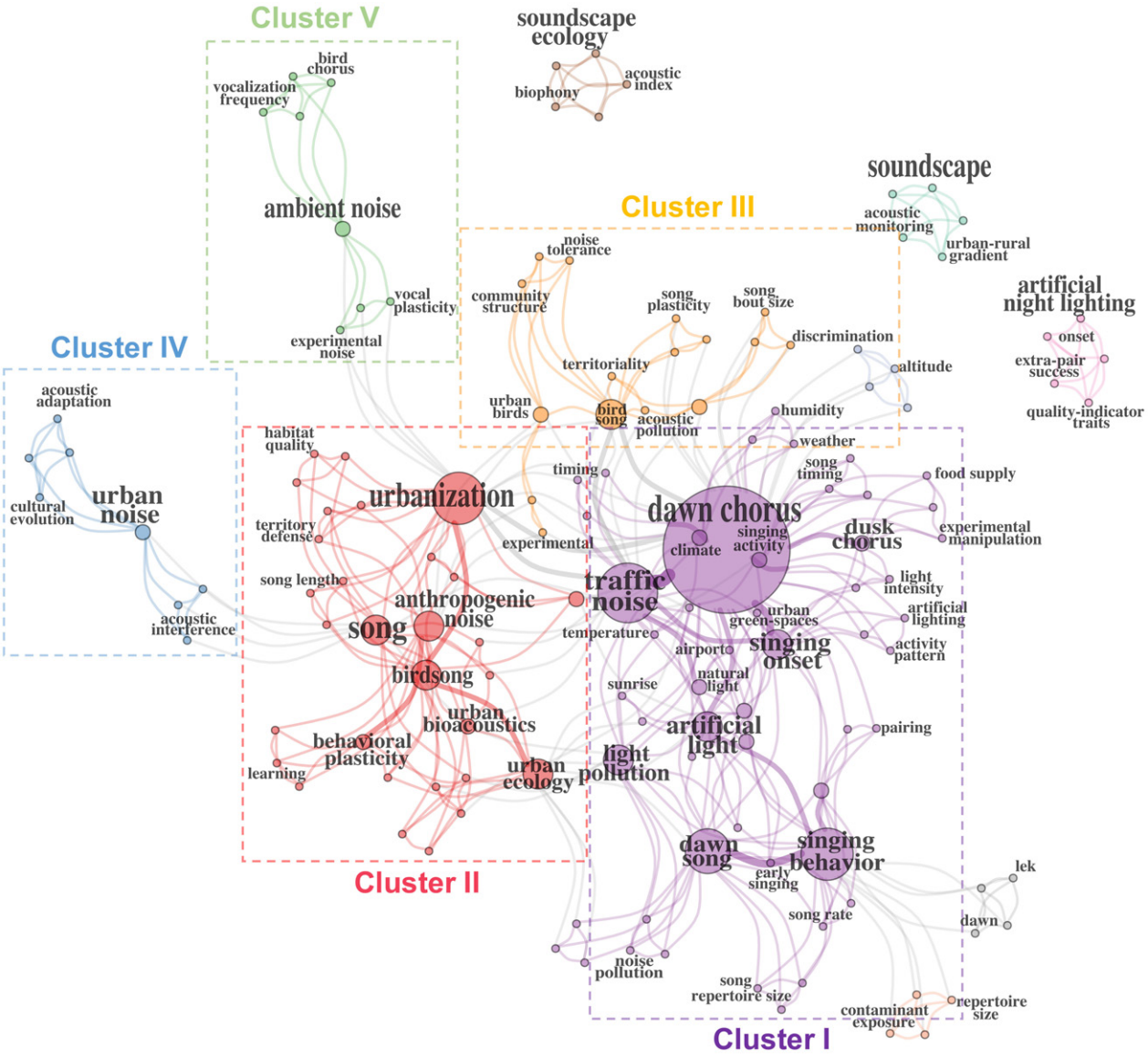

Figure 5. Co-word network for urban dawn chorus studies showing the most frequently studied topics via author keywords (n = 50). Some keywords were omitted to avoid overlapping terms. Node size represents keyword frequency and links the frequency of keyword co-occurrence. Colours represent clusters of keywords with a high degree of connectedness

Studies of the role of noise pollution on dawn chorus behaviour have focused on airports due to the opportunity they provide to disentangle the influence of higher levels of noise in the absence of other urban-related confounding factors. Results from such studies have provided important evidence of changes in dawn chorus timing driven by intermittent and predictable high noise levels in a broad range of frequencies (Gil *et al.* 2015, Sierro *et al.* 2017). In general, birds living near airports show earlier dawn chorus onsets to avoid peak noise periods in the early morning (Gil & Brumm 2014, Dominoni *et al.* 2016, Sierro *et al.* 2017). However, the magnitude of such change can vary among species due to differential tolerance to noise levels; some species can be either earlier or later singers (Gil *et al.* 2015, Dominoni *et al.* 2016), although tropical birds seem to be less

affected by exposure to airport noise (Alquezar 2018). For example, when considering studies from temperate regions, nearly half of the studied species have earlier chorus onsets (Gil *et al.* 2015, Dominoni *et al.* 2016), whereas in tropical sites, only two of 15 studied species showed significant advances in their dawn chorus onset (Alquezar 2018).

Light pollution

ALAN is a global ecological change that has received research attention in recent years due to its interference with circadian rhythms and the selective pressures it imposes on organisms in cities (Hopkins *et al.* 2018). In fact, ALAN has been suggested to be an important threat to nocturnal migratory bird species, as well as a driver of avian behavioural change and reproductive success in cities (Kempenaers *et al.* 2010, Isaksson 2018). Field experiments suggest that light pollution can disrupt sleep (Raap *et al.* 2015), as well as the daily singing routines of birds (Da Silva *et al.* 2016, 2017). For example, forest songbirds adjust the timing of their dawn choruses to the experimental manipulation of artificial light levels (Da Silva *et al.* 2016). However, a recent study showed that experimental illumination of a forest using lights of different colours had no effect on the dawn chorus timing of 14 temperate songbird species (Da Silva *et al.* 2017). These studies were performed outside urban areas to avoid confounding urbanization effects such as built and vegetation covers, noise pollution, increased temperatures, and altered food supply (Da Silva *et al.* 2017).

Correlative studies of ALAN have provided evidence of earlier dawn chorus onsets in light-polluted urban sites (Miller 2006, Shihan 2010, Nordt & Klenke 2013, Ki & Cho 2014), which also interact synergistically with noise pollution (Bergen & Abs 1997, Nordt & Klenke 2013, Dominoni *et al.* 2020a). Given that songbirds are capable of adjusting their dawn chorus onsets to variations of both natural and artificial light levels (Leopold & Enyon 1961, Da Silva *et al.* 2016, Lee *et al.* 2017), the effects of ALAN are expected to be strong in cities at high latitudes where the daily photoperiod varies across the year (Da Silva & Kempenaers 2017). The effects of ALAN are also expected to affect earlier-singing songbirds (Edenborg 2018). Interestingly, the few recent studies performed in tropical cities have found no relationships between dawn chorus onsets and ALAN at the population- (Dorado-Correa *et al.* 2016) or community-level (Marín-Gómez & MacGregor-Fors 2019), suggesting that ALAN does not seem to represent a driver of the singing routines of tropical urban birds.

Chemical pollution

Although chemical pollution is an important influence on urban avian ecology (Isaksson 2018), we found only one study exploring its impact on chorus onset and song output (Gorissen *et al.* 2005). This study found that Great Tits exposed to higher levels of heavy metal pollution showed smaller repertoire size and lower song rate during their dawn chorus. Environmental pollution may therefore influence song production by constraining available time and energy budgets for vocal activity (Gorissen *et al.* 2005).

Meteorological factors

Evidence from Middle Eastern cities suggests that time changes in dawn choruses (i.e. earlier onset) are associated with higher environmental temperatures (Hasan 2010). Other meteorological variables, such as higher wind, precipitation and cloudiness, and lower temperatures have also been suggested to delay dawn chorus onsets (Leopold & Enyon 1961, Nordt & Klenke 2013, Hasan & Badri 2016). For instance, longer days, together with high temperatures during summer, can lead to earlier House Sparrow dawn chorus onsets (Hasan & Badri 2016), and Nordt and Klenke (2013) suggest that cloud cover in cities could act as a reflector that can amplify the sky luminance produced by city lighting and thus increase the effects of ALAN on advancing the dawn chorus onset of Common Blackbirds. This suggestion shows how the interaction between environmental and anthropogenic variables may affect avian dawn chorus timing.

Another important environmental factor related to avian dawn choruses is lunar phase (York *et al.* 2014). Findings of non-urban studies suggest that birds show earlier dawn chorus with moonlight presence at dawn (i.e. full or three-quarter moon; Bruni *et al.* 2014, York *et al.* 2014). Yet this effect varies among species, and seasonally. For example, American Robins sing much earlier during moonlight at the beginning of spring but not during summer (Leopold & Enyon 1961). However, other

studies have shown no correlation between dawn chorus onset and lunar phase or cloud cover in urban settings (Ki & Cho 2014, Ki *et al.* 2015). Perhaps the most important meteorological variable related to dawn chorus timing is variation of light intensity at dawn. As light levels increase before sunrise, bird species join dawn choruses in a specific time window due to differences in species' sensitivity to light (Thomas *et al.* 2002, Berg *et al.* 2006, Chen *et al.* 2015). For example, a recent study performed in urban greenspaces of Los Angeles (CA, USA) showed that light levels could influence the timing of dawn chorus activity (Lee *et al.* 2017).

Supplementary feeding

Much evidence suggests that food supply is a main influence on the ecology of urban birds (Amrhein 2014). Among other effects, supplementary feeding can enhance territoriality and increase song output (Cuthill & Macdonald 1990, Amhrein 2014). Consequently, social hierarchies can be influenced by body mass differences between dominant and subordinate birds, particularly at dawn (Grava *et al.* 2009). Two studies from peri-urban greenspaces have explored the effects of supplementary feeding on dawn chorus onset and song structure. One of them showed that Common Blackbirds sang earlier at dawn and had greater song output when supplemented with food, due to the influence of energetic requirements on male phenotypic condition (Cuthill & Macdonald 1990). In contrast, another study showed the inverse pattern for Great Tits, with individuals under continuous food supply conditions showing delayed dawn chorus onsets (Saggese *et al.* 2011). This unexpected result was explained by the presence of predators at feeding stations and the suboptimal energetic quality of the food supply, as predicted by formal models of daily singing and foraging routines in birds (Hutchinson 2002).

Soundscape ecology

Recent advances in soundscape ecology have highlighted the value of avian dawn and dusk choruses because their predominance in multiple soundscapes around the world and the information included in them can be used to explore the impacts of anthropogenic global driving forces on biodiversity (Krause & Farina 2016). Studies have suggested that avian dawn choruses are important indicators of soundscape structure across urbanization gradients (Gage *et al.* 2017, Ross *et al.* 2018). For example, a study from peri-urban Brisbane (Australia) showed that avian dawn choruses can be identified by abrupt changes of energy power, as revealed by acoustic indices (Gage *et al.* 2017). Moreover, a recent study that explored the impact of urbanization on soundscape patterns in Okinawa (Japan) also suggests a relationship between some acoustic indices and temporal variations in avian choruses across urban gradients (Ross *et al.* 2018).

FUTURE DIRECTIONS AND CONCLUSIONS

In this review we have synthesized the available knowledge on the impacts of urbanization on an emergent property of the behaviour of many individual birds of multiple species – the dawn chorus. Beyond previous reviews on the topic outside urban settings that provide general explanations of why birds sing at dawn (Staicer *et al.* 1996, Catchpole & Slater 2008, Gil & Llusia 2020), our findings show short-term adjustments in the timing, song frequency, song repertoire and syntax in response to urban noise; earlier dawn chorus onsets in light-polluted urban sites; smaller repertoire size and lower song rate in sites exposed to chemical pollution; and increase of song output and delayed chorus onsets because of supplementary feeding. Our results also shed light on important future research directions.

Due to the biological importance of dawn choruses in territorial signalling and reproductive success (Staicer *et al.* 1996), most research has focused on understanding how anthropogenic noise affects the structure and temporal traits of songs emitted during this critical period. As result, most of the reviewed studies suggest significant changes in different song traits at dawn. Additionally, although correlative and experimental studies have shown how birds increase the minimum frequency of dawn songs to increase sound transmission in noisier urban environments (Ripmeester *et al.* 2010, Potvin *et al.* 2011, Potvin & Parris 2012, Rios-Chelen *et al.* 2013), the mechanisms behind such patterns are not well understood. Moreover, not all bird species respond in a similar fashion to urban noise. Short-term and non-adaptive changes (e.g. acoustic plasticity) are well

documented (e.g. Ripmeester *et al.* 2010, Arroyo-Solís *et al.* 2013, Gil *et al.* 2014, LaZerte *et al.* 2017), whereas evolutionary responses, such as cultural evolution of song, have received less attention (e.g. Luther & Baptista 2010, Potvin *et al.* 2011, Potvin & Parris 2012). Thus, we encourage future studies to assess the consequences of those adjustments on individual fitness. In fact, whether acoustic phenotype adjustments driven by urbanization are adaptive or not remains a controversial issue in urban avian ecology (Nemeth & Brumm 2010, Slabbekoorn *et al.* 2012, Gil & Brumm 2014).

The timing of dawn choruses is affected not only by urban-related stressors (anthropogenic noise, ALAN) and meteorological factors, but also potentially by the abundance of conspecific neighbours (Hodgson *et al.* 2018, Stuart *et al.* 2019), perceived predation risk (Santema *et al.* 2019), body condition (Kacelnik & Krebs 1982) and transmission properties of the urban environment (Phillips *et al.* 2020). Predation pressure has been shown to increase with urbanization (Fischer *et al.* 2012); yet, potential influences of predation on dawn chorus timing remain untested. Additionally, although supplementary feeding is widespread in cities and can alter avian body condition (Amrhein 2014, Phillips *et al.* 2018, Baverstock *et al.* 2019), the effects of feeders on dawn chorus timing remain controversial, so that a larger sample of studies of its impacts would be valuable.

Given the multifunctional nature of the dawn chorus, experimental studies combining controlled noise exposure, experimental light conditions and food provisioning treatments could shed light on the mechanisms related to dawn chorus adjustments (Arroyo-Solís *et al.* 2013, Marini *et al.* 2017). For instance, there is a pressing need to understand the mechanisms behind the identified patterns, such as physiological mechanisms (i.e. how does artificial light pollution affect avian circadian rhythms across latitudes? e.g. Da Silva & Kempenaers 2017), behavioural mechanisms (i.e. do short-term responses, phenotypic plasticity or cultural evolution drive dawn chorus timing or structure? e.g. Gil & Brumm 2014) and ecological mechanisms (i.e. how do bird communities from heavily urbanized sites use the acoustic space differently from non-urban communities? e.g. Marín-Gómez *et al.* 2020).

Tackling geographical bias is also crucial to developing further an understanding of the patterns and processes of urban dawn choruses. Currently, the main body of knowledge comes from studies conducted in the Palearctic and Nearctic regions, with substantial information only for a few species. Therefore, more studies from a more representative sample of regions and species are needed to understand the factors driving dawn chorus adjustments.

We consider that assessing avian dawn choruses in cities at the community-level could provide important insights into the use of the acoustic space by bird communities in different urbanization conditions, and in particular, how urbanization could change the structure of dawn choruses and how exotic species use the acoustic space and potentially limit the signalling of native species. For example, a recent study in a neotropical city compared the structure of the avian dawn choruses at the community-level in both intra-urban and peri-urban areas (Marín-Gómez *et al.* 2020). The findings of that study suggested a modular structure of avian dawn choruses in peri-urban areas (i.e. groups of co-occurring bird species singing at different times through the morning) supporting the temporal partitioning of the acoustic space, but the loss of the temporal order of dawn choruses at intra-urban areas related to the depauperization of the avian community together with the dominance of the acoustic space by invasive species (Marín-Gómez *et al.* 2020). This study calls for the need to consider the influence of different sources of noise in urban settings and its influence on the partitioning of the acoustic space.

Although we identified studies from cities of differing sizes, there is an under-representation of evidence from megacities, contrasting with a preponderance of data from megacities in other arenas of urban ecology. Currently, most studies are based on urban–non-urban contrasts, with few considering urbanization intensity gradients (e.g. Marini *et al.* 2017, Ross *et al.* 2018). Thus, to understand acoustic phenotype adjustments to urbanization, studies should include survey sites across urbanization intensity gradients. This would better represent the differing acoustic transmission traits across cities (e.g. Phillips *et al.* 2020) by considering their environmental heterogeneity. Thus, future studies should consider urbanization intensity gradient frameworks to explore the influence of a wider array of urbanization conditions on avian dawn singing routines.

We were surprised to find no study assessing relationships between increasing temperature in cities (i.e. urban heat islands) and singing behaviour and sound transmission across urban to non-urban gradients. High temperatures have been shown to correspond to earlier dawn chorus onsets (e.g. Hasan 2010, Hasan & Badri 2016), but the associated mechanisms remain unknown. In some cities from Saudi Arabia and Palestine, for instance, where daily temperatures typically exceed 30 °C, House Sparrow singing routines start earlier to avoid higher temperatures during mornings (Hasan & Badri 2016). High temperatures can also advance the breeding season and stimulate earlier dawn chorus onsets (Dominoni *et al*. 2020b), but they may also constrain sound transmission by increasing the absorption of lower frequencies (Farina 2013). Under climate change, and with the increasing role of urban heat islands, we suggest that high temperatures, together with noise and artificial light pollution, may disrupt the circadian rhythms of urban birds and change their singing routines.

Finally, we consider that attention should importantly be paid to the recent boom of soundscape ecology studies and the use of passive acoustic monitoring as a tool to evaluate biodiversity through soundscapes (Farina & Caeraulo 2017). Such technologies and procedures will allow the generation of a significant amount of data that would allow us better to understand the influence of urbanization on avian choruses at all levels of organization at larger scales. As bird dawn choruses are a fundamental component of urban soundscapes and provide multiple cultural services, we forecast an increase in their importance in urban ecological studies, as well as management and planning strategies directed toward fostering sustainable and healthier cities (McDonnell & MacGregor-Fors 2016).

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AUTHOR CONTRIBUTIONS

Oscar Humberto Marín Gómez: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing-original draft (lead); Writing-review & editing (lead). **Ian MacGregor-Fors:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Writing-original draft (supporting); Writing-review & editing (supporting).

REFERENCES

Alquezar, R.D. 2018. *Efeitos da poluição sonora nas características do canto e na fisiologia das aves*. Brasília: Universidade de Brasília.

Amrhein, V. 2014. Wild bird feeding (probably) affects avian urban ecology. In Gil, D. & Brumm, H. (eds) *Avian Urban Ecology*: 29–37. Oxford: Oxford Scholarship.

Aria, M. & Cuccurullo, C. 2017. Bibliometrix: An R-tool for comprehensive science mapping analysis. *J. Informetr.* **11**: 959–975.

Arroyo-Solis, A., Castillo, J.M., Figueroa, E., Lopez-Sanchez, J.L. & Slabbekoorn, H. 2013. Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *J. Avian Biol.* **44**: 288–296.

Baverstock, S., Weston, M.A. & Miller, K.K. 2019. A global paucity of wild bird feeding policy. *Sci. Total Environ.* **653**: 105–111.

Berg, K.S., Brumfield, R.T. & Apanius, V. 2006. Phylogenetic and ecological determinants of the neotropical dawn chorus. *Philos. Trans. R. Soc. B* **273**: 999–1005.

Bergen, F. & Abs, M. 1997. Verhaltensökologische Studie zur Gesangsaktivität von Blaumeise (*Parus caeruleus*), Kohlmeise (*Parus major*) und Buchfink (*Fringilla coelebs*) in einer Großstadt. *J. Ornithol.* **138**: 451–467.

Bermúdez-Cuamatzin, E., López-Hernández, M., Campbell, J. & Zuria, I. 2018. The role of singing style in song adjustments to fluctuating sound conditions: A comparative study on Mexican birds. *Behav. Process* **157**: 645–655.

Brown, T.J. & Handford, P. 2003. Why birds sing at dawn: the role of consistent song transmission. *Ibis* **145**: 120–129.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J Anim. Ecol.* **73**: 434–440.

Bruni, A., Mennill, D.J. & Foote, J.R. 2014. Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. *J. Ornithol.* **155**: 877–890.

Burivalova, B.Z., Game, E.T. & Butler, R.A. 2019. The sound of a tropical forest. *Science* **363**: 8–9.

Burt, J.M. & Vehrencamp, S.L. 2005. Dawn chorus as an interactive communication network. In McGregor, P.K. (ed) *Animal Communication Networks*: 320–343. Cambridge: Cambridge University Press.

Catchpole, C.K. & Slater, P.J.B. 2008. *Bird Song: Biological Themes and Variations*. New York: Cambridge University Press.

Chen, W., Lee, Y., Tsai, C., Yao, C., Chen, Y., Li, S. & Kuo, Y. 2015. Dawn chorus variation in East-Asian tropical

montane forest birds and its ecological and morphological correlates. *Contrib. Zool.* **84**: 255–265.

Cuthill, I. & Macdonald, W. 1990. Experimental manipulation of the dawn and dusk chorus in the Blackbird *Turdus merula*. *Behav. Ecol. Sociobiol.* **26**: 209–216.

Da Silva, A., de Jong, M., van Grunsven, R.H.A., Visser, M.E., Kempenaers, B. & Spoelstra, K. 2017. Experimental illumination of a forest: no effects of lights of different colours on the onset of the dawn chorus in songbirds. *R. Soc. Open Sci.* **4**: 160638.

Da Silva, A. & Kempenaers, B. 2017. Singing from North to South: Latitudinal variation in timing of dawn singing under natural and artificial light conditions. *J. Anim. Ecol.* **86**: 1286–1297.

Da Silva, A., Valcu, M. & Kempenaers, B. 2016. Behavioural plasticity in the onset of dawn song under intermittent experimental night lighting. *Anim. Behav.* **117**: 155–165.

Dominoni, D.M. 2015. The effects of light pollution on biological rhythms of birds: an integrated, mechanistic perspective. *J. Ornithol.* **156**: 409–418.

Dominoni, D.M., Greif, S., Nemeth, E. & Brumm, H. 2016. Airport noise predicts song timing of European birds. *Ecol. Evol.* **6**: 6151–6159.

Dominoni, D.M., Kjellberg Jensen, J., de Jong, M., Visser, M.E. & Spoelstra, K. 2020b. Artificial light at night, in interaction with spring temperature, modulates timing of reproduction in a passerine bird. *Ecol. Appl.* **30**: e02062.

Dominoni, D., Smit, J.A., Visser, M.E. & Halfwerk, W. 2020a. Multisensory pollution: Artificial light at night and anthropogenic noise have interactive effects on activity patterns of Great Tits (*Parus major*). *Environ. Pollut.* **256**: 113314.

Dorado-Correa, A.M., Rodriguez-Rocha, M. & Brumm, H. 2016. Anthropogenic noise, but not artificial light levels predicts song behaviour in an equatorial bird. *R. Soc. Open Sci.* **3**: 160231.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**: 1969–1973.

Edenborg, F. 2018. *Artificial light at night causes advanced initiation of dawn song in songbirds in Linköping*. Linköping: Linköping University.

Farina, A. 2013. *Soundscape Ecology: Principles, Patterns, Methods and Applications*. Berlin: Springer Science & Business Media.

Farina, A. & Ceraulo, M. 2017. The acoustic chorus and its ecological significance. In Farina, A. & Gage, S.H. (eds) *Ecoacoustics: The Ecological Role of Sounds*: 81–89. London: John Wiley and Sons.

Fischer, J.D., Cleeton, S.H., Lyons, T.P. & Miller, J.R. 2012. Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience* **62**: 809–818.

Fuller, R.A., Warren, P.H. & Gaston, K.J. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biol. Lett.* **3**: 368–370.

Gage, S.H., Wimmer, J., Tarrant, T. & Grace, P.R. 2017. Acoustic patterns at the Samford ecological research facility in South East Queensland, Australia: The peri-urban supersite of the terrestrial ecosystem research network. *Ecol. Inform.* **38**: 62–75.

Gaston, K.J., Davies, T.W., Nedelec, S.L. & Holt, L.A. 2017. Impacts of artificial light at night on biological timings. *Annu. Rev. Ecol. Evol. Syst* **48**: 49–68.

Gil, D. & Brumm, H. 2014. *Avian Urban Ecology*. Oxford: Oxford University Press.

Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E. & Macías Garcia, C. 2015. Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behav. Ecol.* **26**: 435–443.

Gil, D. & Llusia, D. 2020. The bird dawn chorus revisited. In Mathevon, N. & Aubin, T. (eds) *Coding Strategies in Vertebrate Acoustic Communication*: 45–90. Cham: Springer.

Gorissen, L., Snoeijs, T., Duyse, E.V. & Eens, M. 2005. Heavy metal pollution affects dawn singing behaviour in a small passerine bird. *Oecologia* **145**: 504–509.

Grava, T., Grava, A. & Otter, K. 2009. Supplemental feeding and dawn singing in Black-Capped Chickadees. *Condor* **111**: 560–564.

Greenfield, M.D. 2005. Mechanisms and evolution of communal sexual displays in arthropods and anurans. *Adv. Study Behav.* **35**: 1–62.

Haddaway, N.R., Collins, A.M., Coughlin, D. & Kirk, S. 2015. The role of Google Scholar in evidence reviews and its applicability to grey literature searching. *PLoS One* **10**: e0138237.

Halfwerk, W., Lohr, B. & Slabbekoorn, H. 2018. Impact of man-made sound on birds and their songs. In Slabbekoorn, H., Dooling, R.J., Popper, A.N. & Fay, R.R. (eds) *Effects of Anthropogenic Noise on Animals*: 209–242. Berlin: Springer Handbook of Auditory Research.

Halfwerk, W. & Slabbekoorn, H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Anim. Behav.* **78**: 1301–1307.

Hasan, N.M. 2010. Comparison of the onset of dawn chorus of Bulbuls and House Sparrows in two different geographical locations: effect of climate, noise and light pollution. *Res. Opin. Anim. Vet. Sci.* **1**: 220–225.

Hasan, N.M. 2011. Effect of seasonal variations, altitude and geographical location on the onset of dawn chorus in three bird species in Middle East. *Open Ornithol. J.* **4**: 30–34.

Hasan, N.M. & Badri, M. 2016. Effect of ambient temperature on dawn chorus of House Sparrows. *Environ. Ecol. Res.* **4**: 161–168.

Hodgson, L., Waas, J.R. & Foote, J.R. 2018. Early singers attend to conspecific but not heterospecific behavioural cues at dawn. *J Avian Biol.* **49**: e01749.

Hopkins, G.R., Gaston, K.J., Visser, M.E., Elgar, M.A. & Jones, T.M. 2018. Artificial light at night as a driver of evolution across urban–rural landscapes. *Front. Ecol. Environ.* **16**: 472–479.

Hutchinson, J.M. 2002. Two explanations of the dawn chorus compared: how monotonically changing light levels favour a short break from singing. *Anim. Behav.* **64**: 527–539.

Isaksson, C. 2018. Impact of urbanization on birds. In Tietze, D.T. (ed) *Bird Species*: 235–257. Berlin: Springer International Publishing.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. 2012. The global diversity of birds in space and time. *Nature* **491**: 44.

Kacelnik, A. & Krebs, J.R. 1982. The dawn chorus in the Great Tit (*Parus major*): Proximate and ultimate causes. *Behaviour* **83**: 287–309.

Kempenaers, B., Borgstro, P., Loe, P., Schlicht, E. & Valcu, M. 2010. Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr. Biol.* **20**: 1735–1739.

Ki, K.S. & Cho, W. 2014. Effects of light pollution and environmental factors on dawn song initiation time of Great Tit. *Parus major. Korean J. Environ. Ecol.* **28**: 411–418.

Ki, K.S., Hong, S.H. & Gim, J.Y. 2015. Environmental factors affecting the start of the dawn chorus of wild birds and the differences between each species. *Korean J. Environ. Ecol.* **29**: 344–352.

Krause, B. & Farina, A. 2016. Using ecoacoustic methods to survey the impacts of climate change on biodiversity. *Biol. Conserv.* **195**: 245–254.

Laiolo, P. 2011a. The Rufous-collared Sparrow *Zonotrichia capensis* utters higher frequency songs in urban habitats. *Rev. Cat. Ornitol.* **27**: 25–30.

Laiolo, P. 2011b. Homogenization of birdsong along a natural-urban gradient in Argentina. *Ethol. Ecol. Evol.* **23**: 274–287.

LaZerte, S.E., Otter, K.A. & Slabbekoorn, H. 2017. Mountain Chickadees adjust songs, calls and chorus composition with increasing ambient and experimental anthropogenic noise. *Urban Ecosyst.* **20**: 989–1000.

LaZerte, S.E., Slabbekoorn, H. & Otter, K.A. 2015. Sounds of the city: The effects of noise on communication in Mountain and Black-Capped Chickadees. Natural Resources and Environmental Studies Institute Research Extension Note 17.

LaZerte, S.E., Slabbekoorn, H. & Otter, K.A. 2016. Learning to cope: vocal adjustment to urban noise is correlated with prior experience in Black-Capped Chickadees. *Philos. Trans. R. Soc. B* **283**: 20161058.

Lee, J.-G.-H., MacGregor-Fors, I. & Yeh, P.J. 2017. Sunrise in the city: disentangling drivers of the avian dawn chorus onset in urban greenspaces. *J. Avian Biol.* **48**: 955–964.

Leopold, A. & Eynon, A.E. 1961. Avian daybreak and evening song in relation to time and light intensity. *Condor* **63**: 269–293.

Luther, D. & Baptista, L. 2010. Urban noise and the cultural evolution of bird songs. *Philos. Trans. R. Soc. B* **277**: 469–473.

Manzanares Mena, L. & Macías Garcia, C. 2018. Songbird community structure changes with noise in an urban reserve. *J. Urban Ecol.* **4**: juy022.

Marín-Gómez, O.H., Dáttilo, W., Sosa-López, J.R., Santiago-Alarcon, D. & MacGregor-Fors, I. 2020. Where has the city choir gone? Loss of the temporal structure of bird dawn choruses in urban areas. *Landsc. Urban Plan.* **194**: 103665.

Marín-Gómez, O.H. & MacGregor-Fors, I. 2019. How early do birds start chirping? Dawn chorus onset and peak times in a Neotropical city. *Ardeola* **66**: 327–341.

Marini, K.L.D., Reudink, M.W., LaZerte, S.E. & Otter, K.A. 2017. Urban Mountain Chickadees (*Poecile gambeli*) begin vocalizing earlier, and have greater dawn chorus. *Behaviour* **154**: 1197–1214.

Marzluff, J.M. 2017. A decadal review of urban ornithology and a prospectus for the future. *Ibis* **159**: 1–13.

McDonnell, M.J. & MacGregor-Fors, I. 2016. The ecological future of cities. *Science* **352**: 936–938.

McDonnell, M.J. & Pickett, S.T.A. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* **71**: 1232–1237.

Miller, M.W. 2006. Apparent effects of light pollution on singing behavior of American Robins. *Condor* **108**: 130–139.

Morton, E.S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* **109**: 17–34.

Nakagawa, S., Samarasinghe, G., Haddaway, N.R., Westgate, M.J., O'Dea, R.E., Noble, D.W. & Lagisz, M. 2019. Research weaving: visualizing the future of research synthesis. *Trends Ecol. Evol.* **34**: 224–238.

Nemeth, E. & Brumm, H. 2010. Birds and anthropogenic noise: are urban songs adaptive? *Am. Nat.* **176**: 465–475.

Nordt, A. & Klenke, R. 2013. Sleepless in town – drivers of the temporal shift in dawn song in urban European Blackbirds. *PLoS One* **8**: e71476.

Phillips, J.N., Gentry, K.E., Luther, D.A. & Derryberry, E.P. 2018. Surviving in the city: higher apparent survival for urban birds but worse condition on noisy territories. *Ecosphere* **9**: e02440.

Phillips, J.N., Rochefort, C., Lipshutz, S., Derryberry, G.E., Luther, D. & Derryberry, E.P. 2020. Increased attenuation and reverberation are associated with lower maximum frequencies and narrow bandwidth of bird songs in cities. *J. Ornithol.* **161**: 593–608.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L. & Krause, B.L. 2011. What is soundscape ecology? An introduction and overview of an emerging new science. *Landsc. Ecol.* **26**: 1213–1232.

Pizo, M.A. & Silva, W.R. 2001. The dawn lek of the Swallow-Tailed Hummingbird. *Wilson J. Ornithol.* **113**: 388–397.

Potvin, D.A. & Parris, K.M. 2012. Song convergence in multiple urban populations of Silvereyes (*Zosterops lateralis*). *Ecol. Evol.* **2**: 1977–1984.

Potvin, D.A., Parris, K.M. & Mulder, R.A. 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in Silvereyes (*Zosterops lateralis*). *Philos. Trans. R. Soc. B* **278**: 2464–2469.

Raap, T., Pinxten, R. & Eens, M. 2015. Light pollution disrupts sleep in free-living animals. *Sci. Rep.* **5**: 13557.

Rios-Chelen, A., Quiros-Guerrero, E., Gil, D. & Macias Garcia, C. 2013. Dealing with urban noise: Vermilion Flycatchers sing longer songs in noisier territories. *Behav. Ecol. Sociobiol.* **67**: 145–152.

Ripmeester, E.A.P., Kok, J.S., van Rijssel, J.C. & Slabbekoorn, H. 2010. Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European Blackbirds. *Behav. Ecol. Sociobiol.* **64**: 409–418.

Rivera-Caceres, K., Macias Garcia, C., Quiros-Guerrero, E. & Rios-Chelen, A.A. 2011. An interactive playback experiment shows song bout size discrimination in the suboscine Vermilion Flycatcher (*Pyrocephalus rubinus*). *Ethology* **117**: 1120–1127.

Ross, S.-R.-P.-J., Friedman, N.R., Dudley, K.L., Yoshimura, M., Yoshida, T. & Economo, E.P. 2018. Listening to ecosystems: data-rich acoustic monitoring through landscape-scale sensor networks. *Ecol. Res.* **33**: 135–147.

Saggese, K., Korner-Nievergelt, F., Slagsvold, T. & Amrhein, V. 2011. Wild bird feeding delays start of dawn singing in the Great Tit. *Anim. Behav.* **81**: 361–365.

Santema, P., Valcu, M., Clinchy, M., Zanette, L. & Kempenaers, B. 2019. Playback of predator calls inhibits and delays dawn singing in a songbird community. *Behav. Ecol.* **30**: 1283–1288.

Schel, A.M. & Zuberbühler, K. 2012. Dawn chorusing in guereza colobus monkeys. *Behav. Ecol. Sociobiol.* **66**: 361–373.

Sethi, V.K., Bhatt, D. & Kumar, A. 2011. The effect of mate removal on dawn singing behaviour in male pied bush chats. *Current Zool.* **57**: 72–76.

Sethi, V.K., Bhatt, D. & Kumar, A. 2012. Dawn singing behavior of a tropical bird species, the Pied Bush Chat *Saxicola caprata*. *J. Appl. Natural Sci.* **4**: 241–246.

Shannon, G., Mckenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., Mcfarland, S. & Wittemyer, G. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev.* **91**: 982–1005.

Shihan, X. 2010. *The effect of artificial lighting at night on activity pattern and vocal behavior of Male Taiwan Whistling Thrush (Myiophoneus insularis*). Taiwan: Taiwan Normal University.

Sierro, J., Schloesing, E., Pavón, I. & Gil, D. 2017. European Blackbirds exposed to aircraft noise advance their chorus, modify their song and spend more time singing. *Front. Ecol. Evol.* **5**: 1–13.

Singh, A., Bhatt, D. & Sethi, V.K. 2019. Singing behaviour of the oriental Magpie Robin (*Copsychus saularis*). *J. Ornithol.* **160**: 185–193.

Singh, M., Kumar, D., Pandey, P., Kumar, K. & Kumar, V. 2011. Ambient noise levels due to dawn chorus at different habitats in Delhi. *Environ. We An Int. J. Sci. Technol.* **6**: 123–134.

Slabbekoorn, H. 2013. Songs of the city: Noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* **85**: 1089–1099.

Slabbekoorn, H. 2018. Soundscape ecology of the Anthropocene. *Acoust. Today* **14**: 42–49.

Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature* **424**: 267.

Slabbekoorn, H., Yang, X.J. & Halfwerk, W. 2012. Birds and anthropogenic noise: Singing higher may matter: (A comment on Nemeth and Brumm, 'Birds and anthropogenic noise: are urban songs adaptive?'). *Am. Nat.* **180**: 142–145.

Staicer, C.E., Spector, D.A. & Horn, A.G. 1996. The dawn chorus and other diel patterns in acoustic signalling. In Kroodsma, D.E. & Miller, E.H. (eds) *Ecology and Evolution of Acoustic Communication in Birds*. 426–453. Ithaca: Cornell University Press.

Stuart, C.J., Grabarczyk, E.E., Vonhof, M.J. & Gill, S.A. 2019. Social factors, not anthropogenic noise or artificial light, influence onset of dawn singing in a common songbird. *Auk* **136**: ukz045.

Thomas, R.J., Székely, T., Cuthill, I.C., Harper, D.G.C., Newson, S.E., Frayling, T.D. & Wallis, P.D. 2002. Eye size in birds and the timing of song at dawn. *Philos. Trans. R. Soc. B* 831–837.

Tobias, J.A., Sheard, C., Seddon, N., Meade, A., Cotton, A.J. & Nakagawa, S. 2016. Territoriality, social bonds, and the evolution of communal signaling in birds. *Front. Ecol. Evol.* **4**: 74.

Trimboli, S.R. 2010. *A comparison of the singing activity of Carolina Wrens (Thryothorus ludovicianus*) in urban and rural settings. Bowling Green, KY: Western Kentucky University.

Warren, P., Katti, M., Ermann, M. & Brazel, A. 2006. Urban bioacoustics: it's not just noise. *Anim. Behav.* **3**: 491–502.

York, J.E., Young, A.J., Radford, A.N. & York, J.E. 2014. Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. *Biol. Lett.* **10**: 20130970.

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